

THE DENTITION OF THE DURHAM PERMIAN PELECYPOD *PERMOPHORUS COSTATUS* (BROWN)

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ABSTRACT. The all-important Upper Magnesian Limestone specimens of *Permophorus* [formerly *Pleurophorus*] *costatus* (Brown) from Byers's Quarry, Durham, upon which King based his controversial diagnosis of the dentition of *Pleurophorus* King, have been located and re-examined. They confirm the belief of earlier authors that King's original description was erroneous and that there is only one cardinal tooth in each valve. Several other Upper Magnesian Limestone specimens of this species in the Kirkby Collection support these conclusions and have been figured. The essential characters of *Pleurophorus* King (renamed *Permophorus* by Chavan) are redefined in the light of these investigations.

THE well-known and common Permian pelecypod *Permophorus costatus* from the Magnesian Limestone of Durham (and its western representative) and the Zechstein of Germany was first described from the Permian Marls of Newtown, near Manchester, as *Arca costata* by Brown in 1841 (p. 66, pl. 6, figs. 34, 35). It was later described by various authors, who assigned it to several different genera, including *Modiola* (by de Verneuil, 1845), *Cypricardia* (by Geinitz, 1846), *Myoconcha* (by Howse, 1848), and *Cardita* (by Geinitz, 1848). Howse (1848, p. 245) noted that the hinge margin of the right valve 'is furnished with a distinct, oblique tooth or callosity, which fits into the corresponding depression in the left valve'. He was in error in assigning Brown's species to *Myoconcha*, however, for this genus has one oblique cardinal tooth, but no elongate posterior tooth. In addition, the acuminate posterior extremity and the mytiliform shape of *Myoconcha* are quite unlike the typical Durham form of this shell.

In 1848 (p. 11) King described a new genus *Pleurophorus* and his short diagnosis, without figures, was published as follows: 'Form inequilateral: cartilage external: anterior adductor muscular impressions deeply excavated, often bounded posteriorly by a ridge: pallial line entire: dentition cardinal and posterior: cardinal teeth two in each valve, diverging inwardly, and interlocking alternately: posterior teeth linear; the receiving tooth in the left valve.' In 1850 King repeated his diagnosis (p. 180) and described and figured specimens of *Pleurophorus costatus* (Brown), designated by him as type species, from both the Middle Magnesian Limestone of Humbleton Hill and Tunstall Hill, near Sunderland (pl. 15, figs. 13-15), and the Upper Magnesian Limestone of Byers's Quarry, near Marsden (pl. 15, figs. 16-20). King's description of the teeth and muscle scars was presumably based on the complementary valves of a mature individual (figs. 16, 17) and a juvenile (figs. 18, 19). The artist, G. B. Sowerby, Junior, clearly showed the two diverging cardinal teeth in all four valves; there is thus no reason to suspect any printing or lithographic errors on the part of either the author or the artist.

It was not long before students of Permian palaeontology began to express their doubts concerning King's observations. McCoy (1855, p. 497) could discover in his specimens 'only the most minute traces of the cardinal teeth represented so strongly in Professor King's figures'. Schauroth (1856, p. 229) could discern one or two tooth-like

elevations on the hinge-plate of his specimens from the German Zechstein, but stated that they were never clearly developed as two separate cardinal teeth in each valve, as King had described. Howse (1858, p. 36) denied the existence of a second cardinal tooth, while Geinitz (1861, p. 71) cautiously expressed the view that 'a second cardinal tooth of the type clearly illustrated by King appears to be rare' (free translation).

Waagen (1881, pp. 214–15) discussed this problem and concluded that the Salt Range forms of this genus (*Pleurophorus imbricatus* de Koninck, *P. subovalis* Waagen, *P. complanatus* Waagen, and *P. acuteplicatus* Waagen) did indeed possess the distinctive cardinal dentition of King's specimens.

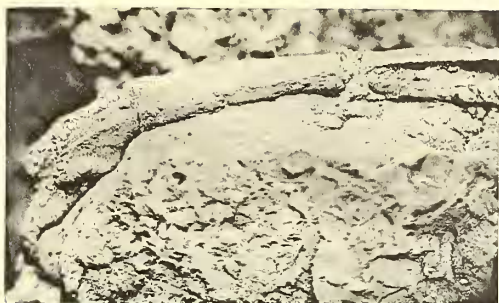
Boehm's studies (1914) of *Pleurophorus* led him to request the loan of King's original specimens from Dr. F. L. Kitchin of the Geological Survey of Great Britain; a search by Dr. Kitchin, however, failed to uncover them. Boehm reports (p. 554) that Kitchin finally sent him a specimen from Tunstall Hill which Boehm illustrated (pl. 21, fig. 4a, b) to support his conclusion that only one cardinal tooth is present in each valve.

Newell (1940, p. 297), describing *Pleurophorus albequus* Beede from the Permian Whitehorse Sandstone of the American Mid-Continent region, gave an excellent discussion of the generic problem involved. He had also begun a search for King's specimens, but failed to ascertain their whereabouts and concluded, mainly from his study of the North American representative of *Pleurophorus*, that King's original diagnosis was probably incorrect. He was able to distinguish only one cardinal tooth in each valve and his detailed and well-illustrated description of *P. albequus* indicates the remarkable similarity of this form to the English Permian form, from which it is distinguished only by its more elongate shape.

Chavan (1954, p. 200), principally from a consideration of *P. albequus* Beede, believed *Pleurophorus* to have a rudimentary second cardinal tooth in each valve and assigned to this genus the lucinoid dental formula 2 (4b) P II / (3a) 3b P III. He also suggested the name *Permophorus* for King's genus, preoccupied by *Pleurophorus* Mulsant 1842, which is in general use by coleopterists (Cox, private communication). Newell (1957, p. 10)

EXPLANATION OF PLATE 47

Figs. 1–9. *Permophorus costatus* (Brown). 1, Hinge of right valve of a mature specimen, showing single cardinal tooth and socket, and slightly grooved postero-lateral tooth, King Collection, Upper Magnesian Limestone, Byers's Quarry, Durham, $\times 5$. 2, Hinge of a mature left valve, with cardinal tooth, King Collection, same locality and horizon as fig. 1, $\times 5$. 3, Hinge of a mature right valve, with cardinal tooth and socket, anterior ridge, pedal retractor pit and anterior adductor muscle shown, King Collection, same locality and horizon as fig. 1, $\times 5$. 4a, Right valve of a poorly preserved mature individual, King Collection, same locality and horizon as fig. 1, $\times 2$. 4b, Cardinal tooth of previous specimen, illuminated from south-west, $\times 2$. 5, Right valve of poorly preserved juvenile specimen, figured by King, 1850, pl. 15, fig. 18, King Collection, same locality and horizon as fig. 1, $\times 5$. 6, Left valve of a juvenile specimen, figured by King, 1850, pl. 15, fig. 19, King Collection, same locality and horizon as fig. 1, $\times 5$. 7, Internal mould of hinge of a mature right valve, illustrating cardinal tooth and socket, anterior ridge, curved pedal retractor pit, and anterior adductor muscle scar, Kirkby Collection, Middle Magnesian Limestone, Humbleton Hill, $\times 4$. 8, Internal mould of hinge of a mature right valve, showing cardinal tooth and socket, anterior ridge and anterior adductor muscle, Kirkby Collection, Upper Magnesian Limestone, Souter Point, Durham, $\times 5$. 9, Internal mould of a mature left valve, showing cardinal tooth and socket and postero-lateral tooth and socket, Kirkby Collection, same locality and horizon as fig. 8, $\times 5$. Figs. 1–6 are in the King Collection, University College, Galway. Figs. 7–9 are in the Kirkby Collection in the Hancock Museum, Newcastle upon Tyne.



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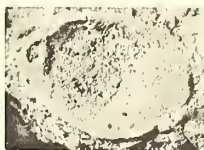
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4a



4b



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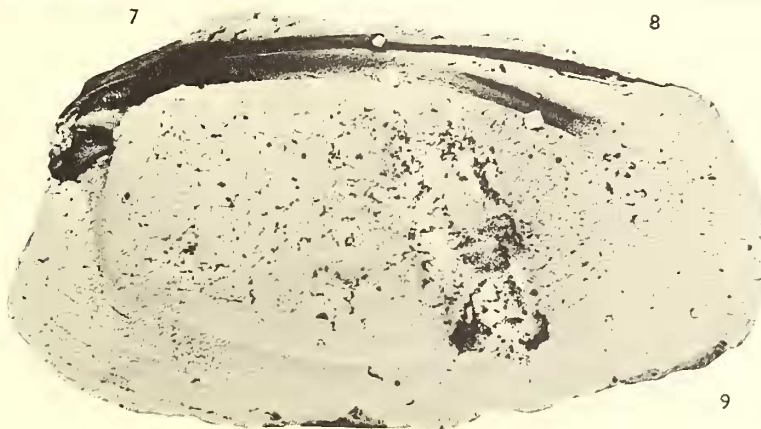
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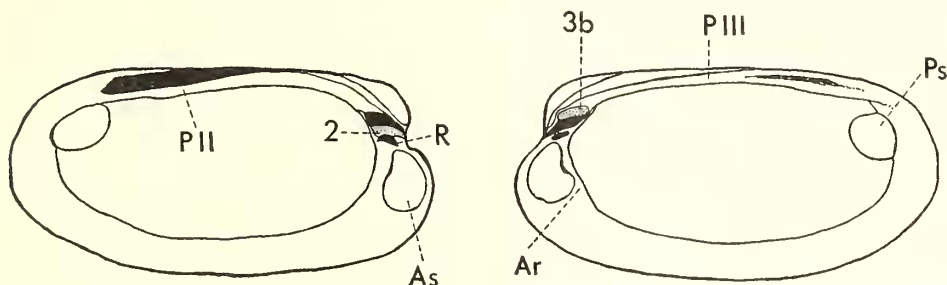
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was unable to confirm cardinal tooth 3a in any of his silicified specimens of *P. albequius* from south-west U.S.A., while 4b and P I were only occasionally present in certain specimens. His dental formula for *Permophorus* was thus: 2 (4b) P II / 3b (P I) P III.

The specimens described and illustrated by King in 1850 from the Upper Magnesian Limestone of Byers's Quarry, Durham, are in the King Collection at University College, Galway, and were kindly loaned by Professor J. L. Mitchell. The shells are rather poorly preserved in the highly calcareous, crystalline facies of the Concretionary Limestone series. In all cases the shells have suffered from partial or complete recrystallization, so that it is often difficult to elucidate the detailed internal structure. King's controversial drawings (figs. 16, 17) are not taken from the two separate valves of a single individual,



TEXT-FIG. 1. Diagrammatic restoration of hinge and musculature of left and right valves of *Permophorus costatus* (Brown), $\times 2$. As, anterior adductor muscle; Ps, posterior adductor muscle; Ar, anterior ridge; R, pedal retractor pit; 2 and 3b, cardinal teeth; P II and P III, postero-lateral teeth. Teeth stippled, sockets black.

but appear to have been reconstructed from several incomplete shells (Pl. 47 figs. 1–4). Similarly, the two juvenile valves illustrated by King (figs. 18, 19) are present on one slab of limestone (although it is not certain that they at one time comprised a single, complete shell), and are so poorly preserved that it is inconceivable that such detail as is depicted in King's figures could possibly be extracted from them (Pl. 47, figs. 5, 6). A single cardinal tooth is well developed in each valve but a close examination of the dentition and musculature in all the specimens available reveals no evidence whatsoever of a second cardinal tooth, however rudimentary, in either valve. The other features, such as the elongate postero-lateral teeth and the small impressions on the anterior ridge (which King attributed to the presence of a visceral or pedal muscle), are easily distinguished, however, and lead one to wonder why the cardinal teeth were so misinterpreted.

A small slab of Upper Magnesian Limestone in the Kirkby Collection, from Souter Point on the Durham coast, about one mile south of Byers's Quarry, showed two internal moulds, one of the left valve and one of the right valve. The shell is no longer present but the hard, fine-grained dolomitic limestone, typical of the Concretionary Limestone series at this locality, has preserved the internal details of these valves to a remarkable degree (Pl. 47, figs. 8, 9). From a study of both King's and Kirkby's specimens (including one well-preserved internal mould from the Middle Magnesian Limestone of Humbleton Hill (Pl. 47, fig. 7)) the dentition of the valves may be elucidated (see text-fig. 1). In the right valve there is a triangular, almost horizontal, ventrally